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Research Article

Comparison between the fish communities of lakes, reservoirs and rivers: can natural systems help define the ecological potential of reservoirs?

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Abstract. The European Water Framework Directive (WFD) aims at improving the ecological status of continental waters, including man-made water bodies. Thereby it raises the question of the reference conditions for reservoirs. A number of limnologists consider reservoirs as intermediate systems between lakes and rivers. Hence, the aim of this study is to contribute to the implementation of the WFD by comparing the fish communities across these three types of ecosystems. This was achieved using fish sampling data from 21 natural lakes, 50 reservoirs and 549 river stations. The lists of occurring species are very similar between lakes and reservoirs, and appear as a subset of the species occurring in rivers. Lakes and reservoirs are also very similar in terms of common and rare species. Conversely, the comparison of community structures (summarised by correspondence analysis axes) supports the hypothesis of an intermediate position of reservoirs between lake and river systems. This latter result could reflect the effect of large-scale processes undergone by freshwater ecosystems whatever their type and the non-independence of water bodies within their catchments, particularly when considering the communities of highly mobile organisms like fishes. Although the major conservation concerns are about natural systems, artificial ones should also be considered in monitoring and assessment programs in order to allow efficient catchment-scale management policies.

Key words. Lentic system; lotic system; fish community; European Water Framework Directive; comparative analysis.

Introduction

The objective of the European Water Framework Directive (WFD) is to obtain the good ecological status of natural continental water bodies and the good "ecological potential" (EP) for artificial and heavily modified water bodies (European Community, 2000). Potentially, various methods can be implemented to define the maximum EP, however, the ECOSTAT working group proposed that "the maximum EP biological conditions should reflect, as far as possible, the biological conditions associated with the closest comparable natural water body type at reference conditions" (ECOSTAT, 2003). Accepting this position raises the question of how to choose the relevant natural hydrosystem type that will serve as a reference for reservoirs, which is a cross-ecosystem question. However, cross-ecosystem studies are not very common despite their interest in addressing the issue of generalisation in ecological patterns, mechanisms and theories (Pace, 1991). For example, cross-ecosystem studies provided a significant contribution to the debate on the relative strength of

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bottom-up vs. top-down controls of food chains (Chase, 2000; Pace et al., 1999; Shurin et al., 2002; Strong, 1992), on the response of ecosystems to disturbances (Fisher and Grimm, 1991) or on fisheries science and management (F.A.O., 1978). These kinds of studies also proved to be informative both on basic and applied issues when comparing freshwater ecosystem types (F.A.O., 1978; Ryder, 1978; Ryder and Pesendorfer, 1989).

Reservoirs are frequently termed artificial lakes and satisfy some of the definition criteria of lakes (Politou et al., 1993). Most of the major processes, i.e. internal mixing, nutrient uptake, primary production or predator-prey interactions, occur in both lakes and reservoirs (Thornton, 1990). However, in a review that contrasted the properties of natural lakes and reservoirs, Wetzel (1990) opposed a long list of ecological, hydrological, physico-chemical and morphological differences between these types of water bodies. Some limnologists also considered reservoirs as intermediate ecosystems between riverine and lacustrine environments (Gelwick and Matthews, 1990; Kimmel et al., 1990; Ryder, 1978) with regard to morphology and hydrology. Reservoirs can also be considered as having an intermediate status with regard to nutrient and organic matter supply (Kimmel et al., 1990).

Comparative ecological studies between rivers and reservoirs are not common in the scientific literature, maybe because they give rise to sampling issues. However, these systems are not so contrasted. River systems typically encompass both lentic and lotic waters and the upper zone of reservoirs is generally riverine (Thornton, 1990). In fact, the transition between typical riverine conditions and truly still waters takes place along a spatio-temporal continuum of hydraulic conditions. Therefore, conventional thresholds are used to define the geographical boundary between a reservoir and its tributaries or to classify the reaches of rivers influenced by a weir as lentic or lotic. However, ecological processes ignore these conventions and the issue of the "closest comparable natural water body" has to be addressed to assess reservoirs reference conditions for each of the biological elements taken into account in the WFD. Although the WFD considers reservoirs as parts of the "lake-type water bodies", there is a risk that referring to lakes to assess the EP of reservoirs without considering alternatives could be a methodological mistake. Therefore, we investigated whether the analyses of fish community patterns in both lakes and rivers could be useful to assess the reference conditions for fish communities of reservoir systems. Thus, we developed a comparative study of the attributes of fish communities in these three types of systems. The hypothesis that reservoirs are intermediate systems between rivers and lakes, considered in a fish community perspective, leads to the hypothesis that they display intermediate patterns of 1. species occurrences 2. species commonness and rarity 3. fish community structure.

Materials and methods

The data set

The lakes and reservoirs data set was compiled from various sources (mostly unpublished study reports). In the absence of a national monitoring network, these studies addressed local concerns. Most of the surveys were carried out with gillnets but we also used fish censuses produced when the reservoirs were drained. Eventually, 50 reservoirs and 21 natural lakes were included. They range from sea level to 1100masl. Mountain lakes and reservoirs have been excluded from the analysis because they have been proven to have very different fish populations compared to lowland sites, mainly as a result of human-mediated introductions (Argillier et al., 2002). A more thorough description of the data set was made in previous papers (Argillier et al., 2002; Irz et al., 2004).

The 549 river stations data were extracted from the database held by the Conseil Supérieur de la Pêche, covering a period of 13 years of survey (1985 to 1998). All sites were sampled using electric fishing techniques during low flow periods. The size of each sampled site was sufficient to encompass complete sets of the local characteristic river habitat (generally >100 m for wading sites and >500 m for boat sites (Yoder and Smith, 1999)). Two main sampling strategies were used, depending on river size. When possible (river depth <0.7 m), river reaches were sampled by wading (one passage). In large rivers, sampling was done by boat mainly in near shore areas. We only retained one fishing occasion per site. Sites belonging to the trout zone and sites characterized by the presence of only two species were excluded.

To limit the biases induced by the differences in sampling methods, fish communities were characterised by the presence/absence of the species. The river stations are well distributed throughout France, but the distribution of lakes and reservoirs is patchier (Figure 1). The main characteristics of the study sites display a strong heterogeneity (Table 1).

Sampling adequacy

One of the major concerns associated with comparisons of very different types of environments is the differences in sampling scheme. No single method allows an accurate fish sampling of both lentic and lotic systems, and it seems that the absence of the eel (*anguilla anguilla*) in both lakes and reservoirs is a consequence of the use of gillnets. The bitterling (*Rhodeus sericeus*) is also frequently too small to be effectively caught by gillnets unless they comprise very fine mesh (which was not the case in our data set, the lower limit generally being 10 mm knot-to-knot).

However, it is quite commonly recognised that gillnetting is the most appropriate technique to sample fishes

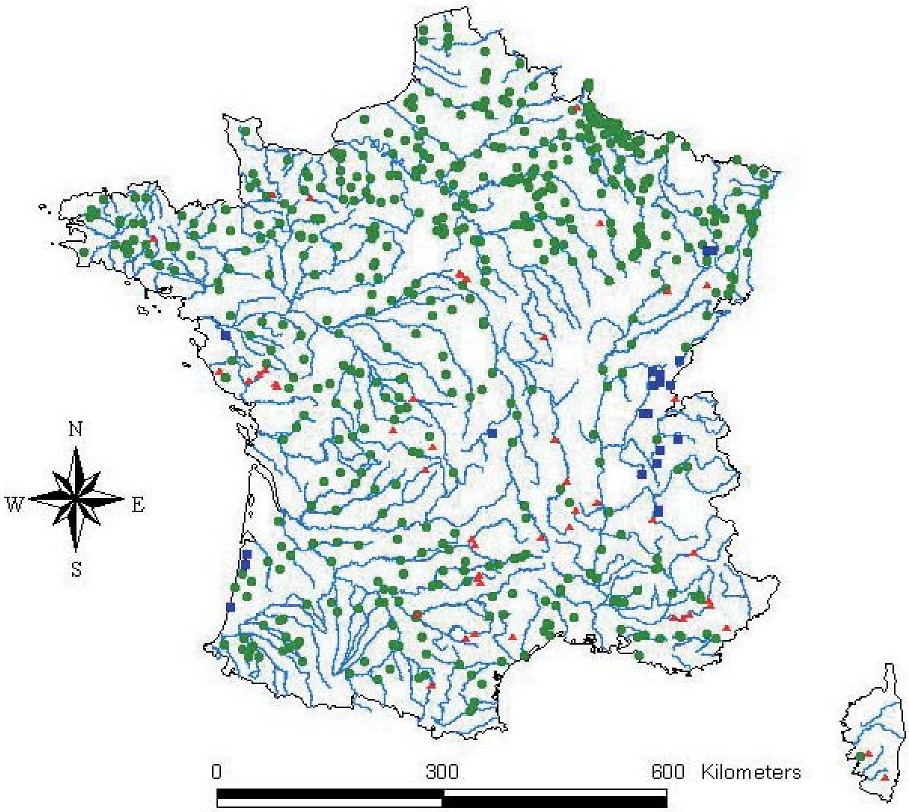

Figure 1. Location of the study sites on the French hydrographic network ■ natural lakes ▲ reservoirs ● river stations.

in lentic systems, as attested by the choice of the European Standardisation Committee to recommend a standardised gillnetting method to implement the WFD on lake-type water bodies (C.E.N., 2005), even though an extensive census of their species should also include complementary techniques in the shallows (US Environmental Protection Agency, 1998). Similarly, electrofishing is the most efficient technique for sampling fish in streams and rivers even if its efficiency decreases when river depth increases. Therefore, our cross-system comparison being based on appropriate techniques for each system type is likely to make sense despite the admitted sampling biases. Using a parallel with Pielou's (1977) consideration on the sampling biases in biogeographic studies, we could state that cross-ecosystem type comparative studies require the assumption that the signal-to-noise ratio of the data is high enough to ensure that, by appropriate statistical analysis, the signal may be recovered and correctly interpreted.

Table 1. Description of the study sites with the mean values, standard deviation and extreme values of the parameters.

	Parameter (unit)	Mean	S. D.	Max	Min
Lakes	Catchment area (km²)	102	168	670	2
N = 21	Altitude (masl)	543	331	1,059	0
	Lake surface (ha)	1,199	2,079	6,500	7
	Maximum depth (m)	37	32	145	2.7
	Lake volume (Mm^3)	286	805	3,614	0.3
Reservoirs	Catchment area (km²)	819	150	6,520	1
N = 50	Altitude (masl)	391	299	1,074	13
	Reservoir surface (ha)	334	565	3,200	4
	Maximum depth (m)	36	33	135	2
	Reservoir volume (Mm^3)	88	235	1,261	0.04
River st.	Catchment area (km²)	2,135	7,354	68,000	2
N = 549	Altitude (masl)	155	142	935	2
	Slope (‰)	2.69	2.83	30	0
	Width (m)	18	34	350	1
	Mean air temperature (°C)	10.8	1.5	16	8

Analyses

The choice was made to use three different descriptors of lacustrine communities (list of occurring species, species occurrence rates and community structure) in order to obtain complementary views on fish community patterns (Samuels and Drake, 1997). The lists of occurring species were simply compared by distinguishing those that were specific of a particular type of environment from those that were more widespread, and by calculating Jaccard's distances between the three types of systems based on the species occurrences.

In order to compare the patterns of rarity or commonness of species among the three types of systems, the relationship between the occurrence rates of the species in lakes, reservoirs and rivers were assessed using Spearman rank correlation. Cross-ecosystem similarities in the identity of the dominant and rare species are expected to produce positive correlations.

Then the fish occurrence matrices were analysed by means of Correspondence Analysis (CA) for each type of system. This ordination method allows a reduction of the dimensionality of the data set (Ter Braak, 1995). Hence, the first two CA axis of each analysis were considered as summaries of a primary and secondary between-site community structure. The six axes were then submitted to Spearman correlation analysis to assess to what extent community structure was similar among system types. To limit the effects of rare species in the analyses, those with occurrence rates below 10 % were removed. All together 30 species were included in at least one of these analyses.

The mean species richnesses were compared among ecosystem type using ANOVA.

All statistical analyses were carried out with SPSS statistical package (SPSS Inc, 1999).

Results

Species occurrences and richnesses

The most common species (pike *Esox lucius*, roach *Rutilus rutilus*, perch *Perca fluviatilis* and tench *Tinca tinca*) are the same in lakes and reservoirs (Table 2). With occurrence rates over 75 %, these four species can be considered ubiquitous in lentic systems. Conversely, no single species attains such a rate in the river stations. The

Table 2. Occurrence rates of the fish species in natural lakes, reservoirs and river stations. Rates over 75 % are in bold.

Code	Common name	Scientific name	% occurrence lakes	% occurrence reservoirs	% occurrence rivers
ALBUAL	Bleak	*Alburnus alburnus*	33.3	40.0	32.2
ANGUAN	Eel	*Anguilla anguilla*	0	0	50.5
BARBFL	Barbel	*Barbus barbus*	0	18.0	32.4
RHODSE	Bitterling	*Rhodeus sericeus*	0	0	12.0
ABRASP	Bream	*Abramis sp.*	71.4	56.0	23.5
ESOXLU	Pike	*Esox lucius*	**95.2**	**78.0**	30.8
CYPRCA	Common carp	*Cyprinus carpio*	23.8	72.0	10.9
COTTGO	Bullhead	*Cottus gobio*	0	0	53.0
LEUCCE	European chub	*Leuciscus cephalus*	66.7	54.0	69.0
CORESP	Whitefish	*Coregonus sp.*	47.6	0	0
GASTAC	Three-spined stickleback	*Gasterosteus aculeatus*	0	0	15.5
PUNGPU	Ninespine stickleback	*Pungitius pungitius*	0	0	11.8
RUTIRU	Roach	*Rutilus rutilus*	**100.0**	**96.0**	60.8
GOBIGO	Gudgeon	*Gobio gobio*	28.6	30.0	72.9
GYMNCE	Ruffe	*Gymnocephalus cernuus*	28.6	26.0	9.1
CHONNA	Sneep	*Chondrostoma nasus*	0	0	13.5
BARBBA	Stone loach	*Barbatula barbatula*	0	0	69.9
LAMPEPL	Brook lamprey	*Lampetra planeri*	0	0	29.0
SALVAL	Arctic char	*Salvelinus alpinus*	19.0	2.0	0
AMEIME	Black bullhead	*Ameiurus melas*	9.5	24.0	7.5
PERCFL	Perch	*Perca fluviatilis*	**95.2**	**96.0**	42.1
LEPOGI	Pumpkinseed	*Lepomis gibbosus*	33.3	46.0	22.8
SCARER	Rudd	*Scardinius erythrophthalmus*	71.4	42.0	16.2
SANDLU	Pikeperch	*Sander lucioperca*	23.8	58.0	6.6
ALBUBI	Chub	*Alburnoïdes bipunctatus*	0	0	16.4
ONCOMY	Rainbow trout	*Oncorhynchus mykiss*	23.8	24.0	5.8
TINCTI	Tench	*Tinca tinca*	**90.5**	**80.0**	21.9
SALMTR	Common trout	*Salmo trutta*	52.4	38.0	58.1
PHOXPH	Eurasian minnow	*Phoxinus phoxinus*	0	0	62.8
LEUCLE	Dace	*Leuciscus leuciscus*	4.8	14.0	41.2

Table 3. Jaccard's distance matrix between the lists of species occurring in each of the three types of hydrosystems.

	lakes	reservoirs	rivers
lakes	0	0.10	0.43
reservoirs	0.10	0	0.38
rivers	0.43	0.38	0

Table 4. Spearman rank correlation between the occurrence rates of species (n = 30) in lakes, reservoirs and river stations. P-values are over the diagonal and correlation coefficients below.

	% lakes	% reservoirs	% rivers
% lakes		<0.001	0.709
% reservoirs	0.869		0.622
% rivers	0.071	0.094	

Table 5. Descriptive statistics of species richness in lakes, reservoirs and river stations.

	Nb	Mean	S.D.	Min	Max
Lakes	21	9.95	4.153	5	20
Reservoirs	50	10.02	3.248	4	16
Rivers	549	9.59	4.254	3	24

most widespread species in lotic systems are the gudgeon *Gobio gobio*, the European chub *Leuciscus cephalus* and the stone loach *Barbatula barbatula*. Ten species are river-specific (eel, bitterling, bullhead *Cottus gobio*, three-spined stickleback *Gasterosteus aculeatus*, ninespine stickleback *Pungitius pungitius*, sneep *Chondrostoma nasus*, stone loach, brook lamprey *Lampetra planeri*, chub *Alburnoïdes bipunctatus* and Eurasian minnow *Phoxinus phoxinus*) while only the whitefish *Coregonus sp.* is lake-specific in this data set (present in 47.6 % of the lakes). All the species found in reservoirs are also present in either or both lakes and rivers. On the basis of Jaccard's index, the lists of occurring species are much more similar between lakes and reservoirs than between lentic systems and rivers (Table 3). The 0.10 distance between lakes and reservoirs (Table 3) indicates that 90 % of the species are common between these types of systems.

The correlation analysis of the occurrence rates of the species among system types (Table 4) confirms that the species that are widespread in lakes are also widespread in reservoirs but that the occurrence rate of species in lotic systems was independent of that in lentic ones.

Therefore, it is clear that more species occur in rivers (28) than in lentic systems (20) although this might be biased due to a higher number of the former than of the latter in our data set, and that both types of lentic systems display very similar patterns of species occurrences. However, there is no significant difference in the mean local species richness among ecosystem types (ANOVA, p = 0.736; Table 5).

Community structure

The first axis (primary structure) of the CA carried out on reservoirs displays an opposition between the arctic char *Salvelinus alpinus* and a group composed of the black bullhead *Ameiurus melas* , ruffe *Gymnocephalus cernuus* and pumpkinseed *Lepomis gibbosus* on the first axis. The secondary structure opposes the dace *Leuciscus leuciscus* to the black bullhead and the arctic char.

The analysis on river stations opposes the brook lamprey, brown trout *Salmo trutta*, ninespine stickleback to the bitterling and bream *Abramis sp.* (Table 6). The second axis (secondary structure) opposes the ninespine stickleback and rudd *Scardinius erythrophthalmus* to the chub, barbel *Barbus barbus* and sneep.

In lakes, the primary structure opposes the black bullhead to the whitefish while the second axis opposes the dace to a group of species such as the ruffe, rudd, and pikeperch *Sander lucioperca.*

The correlations between the species scores on the axis of the three analyses above can be interpreted in terms of cross-ecosystem similaritiy in the community structures (the sign of the coefficients has no meaning because CA axes are not oriented). The first axis of reservoirs was significantly correlated with all four axes of rivers and lakes analyses (Table 7), the strongest correlation being with the first CA axis of lakes. There is also a strong correlation between the second axis of lakes and rivers.

Discussion

Cross-ecosystems comparisons

Our initial hypothesis was that the fish communities of reservoirs would display intermediate patterns between those of lakes and river stations with respect to 1. species occurrences 2. species commonness and rarity 3. fish community structure. Considering the first two points, reservoir fish communities are clearly more similar to the communities of natural lakes than to those of river stations. The lists of species dwelling in the two types of lentic systems are almost identical and clearly divergent from that of rivers. Apart from the two lake specialists (*Salvelinus alpinus* and *Coregonus sp*.), the list of lentic species is a subset of the lotic species list, which is likely to result from historical influences. The western European fish fauna has been quite depauperated since the last ice age drove many species to local extinction. At the scale of a large catchment (i.e., with sufficient latitudinal and/or altitudinal extension), a population of a river species can respond to climatic variations through an adaptation of its

Table 6. Species scores on the first two axes of the CA of fish assemblages performed separately for river stations (F1rivers and F2rivers), lakes and reservoirs. Species codes refer to Table 2.

Code	F1 rivers	F2 rivers	F1 lakes	F2 lakes	F1 reservoirs	F2 reservoirs
ALBUAL	**0.70**	–0.19	–0.51	**0.74**	0.19	**–0.63**
ANGUAN	–0.06	0.22				
BARBFL	0.39	**–0.74**			**1.16**	0.00
RHODSE	**0.92**	–0.08				
ABRASP	**0.92**	0.45	–0.15	–0.14	–0.36	–0.49
ESOXLU	0.42	0.19	0.15	–0.23	–0.24	0.12
CYPRCA	**0.71**	**0.62**	**–0.77**	–0.06	–0.31	0.20
COTTGO	**–0.79**	0.16				
LEUCCE	0.16	–0.18	0.38	0.23	0.58	–0.28
CORESP			**0.70**	0.28		
GASTAC	–0.51	–0.15				
PUNGPU	**–0.90**	**1.12**				
RUTIRU	0.37	0.07	0.18	–0.26	–0.01	0.18
GOBIGO	0.04	–0.15	0.16	**0.83**	**1.09**	0.24
GYMNCE			**–1.04**	–0.48	–0.58	–0.28
CHONNA	**0.65**	**–0.74**				
BARBBA	–0.39	–0.15				
LAMPEPL	**–1.17**	0.45				
SALVAL			–0.02	**0.94**	**2.39**	0.58
AMEIME			**–1.82**	0.05	**–0.88**	**0.66**
PERCFL	0.51	0.24	0.30	–0.26	–0.04	0.13
LEPOGI	**0.67**	0.42	**–0.68**	0.23	–0.50	0.23
SCARER	**0.88**	**0.96**	0.08	–0.32	–0.09	–0.08
SANDLU			**–1.32**	–0.35	–0.39	–0.37
ALBUBI	0.27	**–0.98**				
ONCOMY			**–0.74**	0.58	**0.97**	0.40
TINCTI	**0.72**	**0.66**	0.21	–0.16	–0.05	0.31
SALMTR	**–0.99**	0.05	0.38	0.35	**0.94**	–0.12
PHOXPH	–0.50	–0.28				
LEUCLE	0.19	–0.39	–0.55	**1.69**	–0.20	**–1.46**

Table 7. Spearman rank correlations between the species scores in the CA of fishes occurrences in river stations, lakes and reservoirs. P-values are above the diagonal and correlation coefficients below (*significant at the 0.05 level; **significant at the 0.01 level). The sign of the coefficients has no meaning because CA axes are not oriented. The analysis includes only the species that are common between the two types of systems compared, i. e. for lakes and rivers, n = 13; for lakes and reservoirs, n = 18 and for rivers and reservoirs n = 14.

	F1 rivers	F2 rivers	F1 lakes	F2 lakes	F1 reservoirs	F2 reservoirs
F1rivers		0.42	0.10	0.09	0.02	0.81
F2rivers	0.17		0.66	0.01	0.02	0.10
F1lakes	–0.48	–0.14		0.65	0.01	0.83
F2lakes	–0.48	–0.70**	0.11		0.02	0.59
F1reservoirs	–0.63*	–0.63*	0.63**	0.53*		0.52
F2reservoirs	0.07	0.46	–0.05	0.14	0.16	

geographic range (Gaston, 2003), for example by reaching refugial zones. Conversely, lakes are frequently regarded as biogeographic islands due to their relative isolation from each other (Barbour and Brown, 1974; Magnuson, 1976; Magnuson et al., 1998). Thus, typical lacustrine species have restricted means to escape an environment becoming less and less favourable. Therefore, it appears reasonable to assume that lacustrine species, if they existed in Western Europe before the last ice age, have undergone higher extinction rates than riverine ones.

Furthermore, the post-glacial westward re-colonisation of fishes from the Danubian refugial zones occurred through the hydrographic network, which means that even for those lentic species that maintained populations in refugial zones, re-colonisation through this unfavourable network of flowing waters was unlikely.

The primary structure of reservoir fish communities displays similarities with all four axes of the analysis carried out on rivers and lakes, which supports our initial hypothesis. Drawing conclusions would have been easier with clear correspondences with either and not both the primary or secondary structure of lakes and rivers (e.g. the reservoirs primary structure corresponds to the lakes secondary structure). However, this rather confused pattern of interrelationships between the community structures could reflect the effects of large-scale phenomena on the fish communities. The response to large-scale environmental gradients (e.g. temperature) or the cross-catchments variations in species pools is likely to generate similar patterns whatever the type of ecosystem.

The secondary community structure of reservoirs was correlated with neither lakes' nor rivers' CA axes, thereby indicating a different pattern or an absence of pattern (e.g. this might be due to stochastic events such as human-mediated species introductions or unpredictable water level fluctuations).

Conversely, the secondary structure of fish communities in the two types of natural systems was quite similar, thereby suggesting common underlying processes. Although opposed in terms of hydrology, lakes and rivers share a common natural origin that may account for this similarity. When compared to reservoirs that are "recent" systems (on an ecological time scale) undergoing rapid aging processes (Kubecka, 1993; Popp et al., 1996; Thouvenot et al., 2000), natural systems may be considered as "mature" systems. This means that a number of processes underlying community structure, such as competitive interactions or colonisation events, may not have operated long enough to generate community patterns in reservoirs. Consequently, the observation of natural systems is of no help in analysing the secondary structure of reservoirs' fish communities.

The fact that the patterns in fish community structure are not so contrasted between the three types of ecosystems could further reveal that lakes, rivers and reservoirs are not independent from each other. They are all components of catchments and interconnected in a network. The catchment corresponds to the natural borders within which freshwater fish populations express their dynamics. Several of the species that were found in lakes and reservoirs are considered as typically riverine and do not reproduce in these systems (Penczak and Kruk, 2000). Hence, considering stream reaches, lakes or reservoirs as isolated from each other does not take into consideration the high mobility of fishes compared to most other freshwater organisms, particularly in the Western European context in which the majority of the fishes, even those dwelling lentic systems, are of lotic origin.

Conclusions

The initial hypothesis that reservoirs were intermediate environments between natural lakes and rivers was only partially supported by the results obtained in our study. We highlighted both differences and similarities in the patterns of fish communities among ecosystem types. The conclusions drawn on the basis of species occurrences, commonness and rarity, and community structure were quite different, thereby confirming the complementarity of these descriptors of the communities (that are also likely to respond differently to anthropogenic stresses). To some extent, this is also the spirit of the WFD that states that several attributes of fish communities must be taken into consideration for the assessment of the ecological status of water bodies. Using continuous descriptors of the hydraulic conditions (e.g. water velocity, Froude number) is certainly a perspective that should allow the simultaneous consideration of a wide array of hydrosystems regardless their type.

The present study carried out on fish does not mean that the other biological compartments follow equivalent rules, but suggests that the *a priori* choice of natural lakes as references for reservoirs may be questionable.

Despite the close deadlines scheduled in the implementation of the WFD, the studies aiming at proposing reference conditions for reservoirs are rare as most efforts have been concentrated on natural environments that represent major conservation concerns. However, reservoirs also represent important environments particularly in southern Europe (in France, around 90% of the lake-type water bodies over 50 ha are artificial) that should not be neglected if one wishes an efficient catchment-scale management policy.

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References

Argillier, C., O. Pronier and P. Irz, 2002. Approche typologique des peuplements piscicoles lacustres Français. I. Les communautés des plans d'eau d'altitude supérieure à 150 m. Bulletin Français de Pêche et de Pisciculture **365/366:** 373–387.

Barbour, C. D. and J. H. Brown, 1974. Fish species diversity in lakes. American Naturalist **108:** 473–489.

C.E.N., 2005. Water Quality – Sampling of fish with multi-mesh gillnets. prEN 14757 European standard final draft. 26 pp.

Chase, J. M., 2000. Are there real differences among aquatic and terrestrial food webs? Trends in Ecology & Evolution **15:** 408–412.

ECOSTAT, 2003. Overall approach to the classification of ecological status and ecological potential. Final report, Water Framework Directive Common Implementation Strategy – Working Group 2 A – Ecological Status (ECOSTAT), Rome. 53 pp.

European Community, 2000. Directive 2000/60/EC of the European Parliament and of the Council. Official Journal **L327**.

F.A.O., 1978. Comparative studies on freshwater fisheries, FAO Fisheries Technical Paper **198**, F.A.O., Rome, 46 pp.

Fisher, S. G. and N. B. Grimm, 1991. Streams and disturbance: are cross-ecosystem comparisons useful? In: J. J. Cole, G. Lovett and S. Findlay (eds.), Comparative analyses of ecosystems: patterns, mechanisms, and theories, Springer-Verlag, New York, pp. 196–221.

Gaston, K. J., 2003. The structure and dynamics of geographic ranges, Oxford University Press, Oxford, 276 pp.

Gelwick, F. P. and W. J. Matthews, 1990. Temporal and spatial patterns in littoral-zone fish assemblages of a reservoir (lake Texoma, Oklahoma-Texas, USA). Environmental Biology of Fishes **27:** 107–120.

Irz, P., C. Argillier and T. Oberdorff, 2004. Native and introduced fish species richness in French lakes: local and regional influences. Global Ecology and Biogeography **13:** 335–344.

Kimmel, B. L., O. T. Lind and L. J. Paulson, 1990. Reservoir primary production. In: K. W. Thornton, B. L. Kimmel and F. E. Payne (eds.), Reservoir limnology: ecological perspective, John Wiley & Sons, Inc., New York, U.S.A., pp. 133–193.

Kubecka, J., 1993. Succession of fish communities in reservoirs of central and eastern Europe. In: M. Straskraba, J. G. Tundisi and A. Duncan (eds.), Comparative reservoir limnology and water quality management, Kluwer Academic Publishers, Dortrecht, pp. 153–168.

Magnuson, J. J., 1976. Managing with exotics – a game of chance. Transactions of the American Fisheries Society **105:** 1–9.

Magnuson, J. J., W. M. Tonn, A. Banerjee, J. Toivonen, O. Sanchez and M. Rask, 1998. Isolation vs. extinction in the assembly of fishes in small northern lakes. Ecology **79:** 2941–2956.

Pace, M. L., 1991. Concluding remarks. In: J. J. Cole, G. Lovett and S. Findlay (eds.), Comparative analyses of ecosystems: patterns, mechanisms, and theories, Springer-Verlag, New York, pp. 361–368.

Pace, M. L., J. J. Cole, S. R. Carpenter and J. F. Kitchell, 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution **14:** 483–488.

Penczak, T. and A. Kruk, 2000. Threatened obligatory riverine fishes in human-modified Polish rivers. Ecology of Freshwater Fish **9:** 109–117.

Pielou, E. C., 1977. The latitudinal spans of seaweed species and their patterns of overlap. Journal of Biogeography **4:** 299–311.

Politou, C. Y., P. S. Economidis and A. I. Sinis, 1993. Feeding biology of bleak, *Alburnus alburnus*, in Lake Koronia, northern Greece. Journal of Fish Biology **43:** 33–43.

Popp, A., K. D. Hoagland and G. L. Hergenrader, 1996. Zooplankton community response to reservoir aging. Hydrobiologia **339:** 13–21.

Ryder, R. A., 1978. Ecological heterogeneity between north-temperate reservoirs and glacial lake systems due to differing succession rates and cultural uses. Verhandlungen der Internationalen Vereinigung fuer Limnologie **20:** 1568–1574.

Ryder, R. A. and J. Pesendorfer, 1989. Large rivers are more than flowing lakes: A comparative review. Canadian Special Publications of Fisheries and Aquatic Sciences **106:** 65–85.

Samuels, C. L. and J. A. Drake, 1997. Divergent perspectives on community convergence. Trends in Ecology & Evolution **12:** 427–432.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper and B. S. Halpern, 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters **5:** 785–791.

SPSS Inc, 1999. SPSS base 9.0 – User's guide, SPSS Inc., Chicago, 740 pp.

Strong, D. R., 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology **73:** 747–754.

Ter Braak, C. J. F., 1995. Ordination. In: R. H. G. Jongman, C. J. F. Ter Braak and O. F. R. VanTongeren (eds.), Data analysis in community and landscape ecology, Cambridge University Press, Cambridge, U.K., pp. 91–173.

Thornton, K. W., 1990. Perspectives on reservoir limnology. In: K. W. Thornton, B. L. Kimmel and F. E. Payne (eds.), Reservoir limnology: ecological perspective, John Wiley & Sons, Inc., New York, U.S.A., pp. 1–13.

Thouvenot, A., D. Debroas, M. Richardot, L. B. Jugnia and J. Devaux, 2000. A study of changes between years in the structure of plankton community in a newly-flooded reservoir. Archiv für hydrobiologie **149:** 131–152.

US Environmental Protection Agency, 1998. Lake and reservoir bioassessment and biocriteria. Technical guidance document, Washington, DC. 252 pp.

Wetzel, R. G., 1990. Reservoir ecosystems: conclusions and speculations. In: K. W. Thornton, B. L. Kimmel and F. E. Payne (eds.), Reservoir limnology: ecological perspective, John Wiley & Sons, Inc., New York, USA., pp. 227–238.

Yoder, C. O. and M. A. Smith, 1999. Using fish assemblages in a state biological assessment and criteria program: essential concepts and considerations. In: T. P. Simon (ed.) Assessing the sustainability and biological integrity of water resources using fish communities, Lewis Press, Boca Raton, Florida, pp. 17–57.